

Systematics and Biogeography of the Jellyfish *Aurelia labiata* (Cnidaria: Scyphozoa)

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Abstract. The hypothesis that the common eastern North Pacific *Aurelia* is *A. aurita* is falsified with morphological analysis. The name *Aurelia labiata* is resurrected, and the species is redescribed, to refer to medusae differing from *A. aurita* by a suite of characters related to a broad and elongated manubrium. Specifically, the oral arms are short, separated by and arising from the *base* of the fleshy manubrium, and the planulae are brooded upon the manubrium itself, rather than on the oral arms. *Aurelia aurita* possesses no corresponding enlarged structure. Furthermore, the number of radial canals is typically much greater in *A. labiata*, and thus the canals often appear more anastomosed than in *A. aurita*. Finally, most *A. labiata* medusae possess a 16-scalloped bell margin, whereas the margin is 8-scalloped in most *A. aurita*. Separation of the two forms has previously been noted on the basis of allozyme and isozyme analyses and on the histology of the neuromuscular system. Partial 18S rDNA sequencing corroborates these findings. Three distinct morphotypes of *A. labiata*, corresponding to separate marine bioprovinces, have been identified among 17 populations from San Diego, California, to Prince William Sound, Alaska. The long-undisputed species *A. limbata* may be simply a color morph of *A. labiata*, or a species within a yet-unelaborated *A. labiata* species complex. The first known introduction of *Aurelia cf. aurita* into southern California waters is documented. Although traditional jellyfish taxonomy tends to recognize many species as cosmopolitan or nearly so, these results indicate that coastal species, such as *A. labiata*, may experience rapid divergence among isolated populations, and that the taxonomy of such species should therefore be scrutinized with special care.

Introduction

Perhaps had Darwin not been afflicted with seasickness, he might have noticed the bewildering array of geographically varying jellyfish morphologies. Some of his contemporaries documented species separated by only short distances but differing greatly in appearance (Eschscholtz, 1829; Brandt, 1835, 1838; Agassiz, 1862; Haeckel, 1879, 1880). Morphological distinctions have since been reported for populations of *Cassiopea* from separate islands of the Caribbean (Hummelink, 1968), *Mastigias* in different lakes of Palau (Hamner and Hauri, 1981), and *Aurelia* scyphistomae from various parts of the Thames estuary (Lambert, 1935). In his studies of the genus *Cyanea*, Brewer (1991) reported distinct morphotypes that could be correlated with isolated locations in Long Island Sound, USA; these observations resurrected a long-standing argument about species distribution and recognition criteria of North Atlantic *Cyanea*. Nineteenth-century taxonomists recognized different species, corresponding to a latitudinal gradation, on both sides of the Atlantic. *Cyanea arctica* Peron and Lesueur, 1810, was known as the boreal species from Europe to North America. In the western Atlantic, *C. fulva* L. Agassiz, 1862, was found along the mid-Atlantic states, while the form south of the Carolinas was recognized as *C. versicolor* L. Agassiz, 1862. In the eastern Atlantic, *C. capillata* (Linnaeus, 1746) was established as the northern European species, while *C. lamarckii* Haeckel, 1880, was identified in warmer southern European waters. This pattern of biodiversity was largely overlooked by twentieth-century taxonomists, who often lumped the forms and recognized only *C. capillata* (Mayer, 1910; Bigelow, 1914; Stiasny and van der Maaden, 1943; Kramp, 1961; Calder, 1971; Larson, 1976).

The scarcity of biogeographic studies of jellyfishes may be, in part, attributable to the unclear systematics of these

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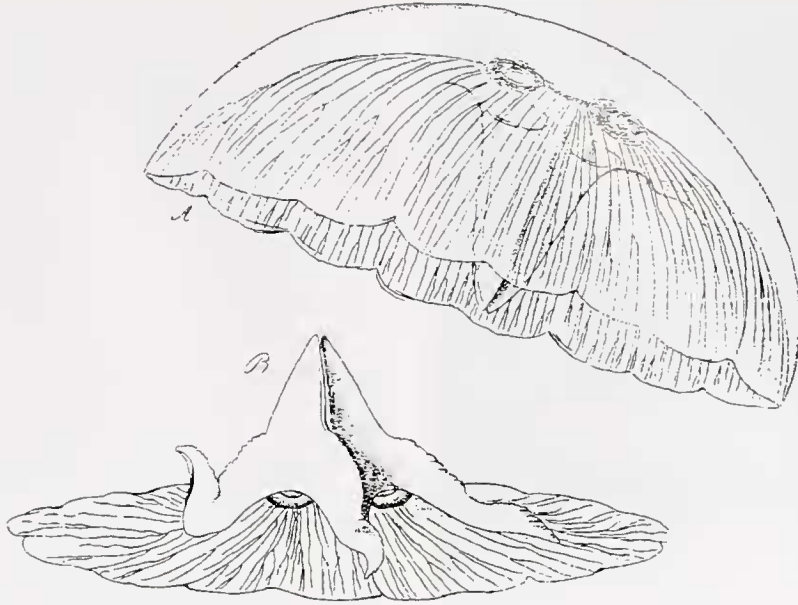


Figure 1. Original illustrations of *Aurelia labiata*, showing greatly enlarged manubrium: (A) lateral view of medusa; (B) oblique view of subumbrella. (Reprinted from Chamisso and Eysenhardt, 1821).

animals. Color differences, patterns of pigmentation, and anatomical variation led to the description of many nominal species during the expeditions of the nineteenth century (see Mayer, 1910; Kramp, 1961). The range of variation in jellyfishes is not well understood, and species definitions are often vague, focusing only on the few most obvious characters. For example, if one sees a flat, whitish medusa with four horseshoe-shaped gonads, most tend to think it must be *Aurelia aurita*. The details of anatomy have not been scrutinized closely. Therefore, significant morphological differences have not been detected, and inappropriate identifications and erroneous conclusions regarding biogeography have been made. The systematic tangle and biogeographic mistakes are common throughout the medusan taxa, though I focus herein on *Aurelia*.

Mayer (1910) recognized 13 unique forms of *Aurellia* (the spelling was later formally changed back to *Aurelia* by Rees, 1957), and sorted these forms into three morphological groups:

1. *A. aurita* (Linnaeus, 1746) sensu Lamarck, 1816, and its seven varieties, described as *A. cruciata* Haeckel, 1880, *A. colpota* Brandt, 1835 [sensu Götte, 1886] (as =*A. coerulea* von Lendenfeld, 1884), *A. flavidula* Peron and Lesueur, 1810 [incorrectly listed as 1809] (as =*A. habanensis* Mayer, 1900), *A. hyalina* Brandt, 1835, *A. dubia* Vanhöffen, 1888, *A. vitiana* Agassiz and Mayer, 1899, and *A. marginalis* L. Agassiz, 1862
2. *A. labiata* Chamisso and Eysenhardt, 1821 [incorrectly listed as 1820], with three varieties, described as

A. clausa Lesson, 1829, *A. limbata* (Brandt, 1835) [incorrectly listed as 1838], and *A. maldivensis* Bigelow, 1904

3. *A. solida* Browne, 1905

Mayer distinguished *A. labiata* and its varieties from the other two groups based primarily on the degree of scalloping of the bell margin, being 16-notched in the former and 8-notched in the latter. He subsequently found a specimen of *A. aurita* at Tortugas, Florida, closely resembling *A. labiata*, leading him to conclude that *A. labiata* was probably derived as a mutation from *A. aurita* (Mayer, 1917). Kramp also wavered on the validity of *A. labiata*, first recognizing the species in his 1961 synopsis, then later regarding it as doubtful (1965, 1968). Most recently, authors such as Russell (1970), Larson (1990), and Arai (1997) have recognized two valid species: *A. limbata*, which is primarily arctic and has a conspicuous brown bell margin, and *A. aurita*, whose name has been treated as the senior synonym of all others. Russell (1970) followed Kramp (1965, 1968) in regarding all other species as varieties, whereas Larson (1990) and Arai (1997) simply did not mention any other species.

The source of this confusion is unclear, as the original description of *A. labiata* was quite specific. Translated from Latin, "It differs from *A. aurita* by its very long oral lips. Marginal tentacles were not observed, but are without a doubt present. Arms appressed to the bell. Diameter of the bell nearly a foot" (Chamisso and Eysenhardt, 1821). The focus of the description and its accompanying illustrations is the strikingly unique elongated manubrium (Figs. 1, 2).

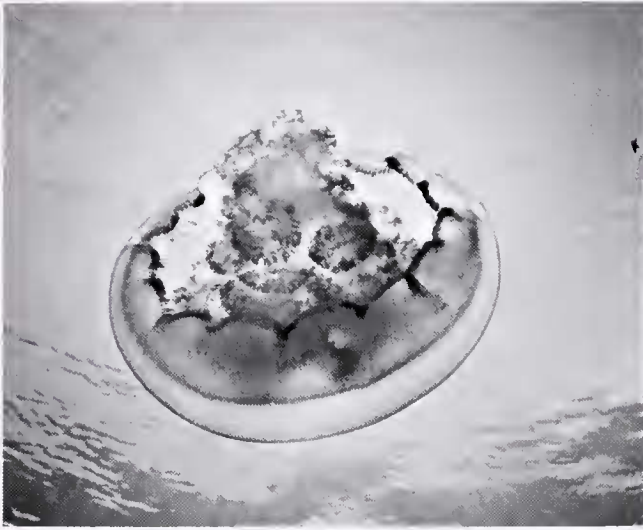


Figure 2. *Aurelia labiata*, adult medusa, from Monterey Bay, California.

although this character is rarely mentioned in later revisions. Furthermore, the characteristically short oral arms arising from the base of the manubrium were mentioned as being held close to the bell, a trait that is readily apparent in live specimens. Ironically, the commonly accepted character of 16 marginal scallops is not mentioned, although it is subtly illustrated. It is unclear why certain key characters of the original description have been ignored by later workers.

Disorder in the nomenclature of *Aurelia* worldwide has caused confusion about the identity of the species in the eastern North Pacific. Depending on the author, one to three species have been recognized. Most authors have applied the name *A. aurita* to all forms. Some distinguish *A. limbata*, although this appears to have been occasionally confused with *A. labiata* (Zubkoff and Lin, 1975; Greenberg *et al.*, 1996). When *A. labiata* has been recognized, it has been separated from *A. aurita* only by the doubling of marginal scallops (Hand, 1975; Kozloff, 1974). Although *A. labiata* was originally described from California, most reports of the species (apparently incorrectly) are from regions outside the eastern North Pacific.

Throughout all the confusion, several studies have reported differences between the eastern North Pacific *Aurelia* and those of other regions, yet failed to elaborate the systematics. Chia *et al.* (1984) found that the muscle system in Puget Sound polyps is distinct from that of polyps from Plymouth, England. Zubkoff and Lin (1975) observed peculiar banding in the isozyme patterns of *Aurelia* scyphistomae from Puget Sound, Washington, that caused them to wonder whether this population may belong to a species other than *A. aurita*. Similarly, Greenberg *et al.* (1996) could distinguish two groups on their allozyme patterns: one group consisted of two populations of *A. "aurita"* from Japan (one from Tokyo Bay, and one aquarium-raised) plus

a population that was apparently introduced to San Francisco Bay; and the second group consisted of wild medusae from Monterey Bay, California, and Vancouver, British Columbia. They further distinguished the two groups on the basis of morphology, using manubrium length and the highly anastomosed condition of the radial canals.

To test the hypothesis that the common eastern North Pacific *Aurelia* is *A. aurita*, I compared the morphology of 17 populations of *Aurelia* from San Diego, California, to Prince William Sound, Alaska, to the morphology of *A. aurita* from Europe, and *A. flavidula* from the eastern United States, as described and figured by Agassiz (1862), Mayer (1910), Kramp (1961), Russell (1970), and many of the references therein. The conclusions that I have drawn on morphological characters are consistent with those emerging from the enzyme analyses of Zubkoff and Lin (1975) and Greenberg *et al.* (1996), the neuromuscular study of Chia *et al.* (1984), and the DNA sequencing results of J. Lowrie of the Cnidarian Research Institute (pers. comm., June 2000)—that is, that the common eastern North Pacific *Aurelia* is not *A. aurita*. However, it does match the description of the species previously described as *Aurelia labiata* Chamisso and Eysenhardt, 1821. Thus, I propose a revalidation of *A. labiata*, and herein offer a redescription and designate a neotype. In scrutinizing the morphology of *A. labiata*, I further found that each population possesses unique characters that cluster into three morphotypes corresponding to well-demarcated biogeographic provinces. The purposes of this paper are to describe the morphological and geographical variation in *A. labiata* and to stabilize the nomenclature for the species. This is necessary as a basis for further systematic investigation, for ongoing biodiversity studies, and for proper management of species introductions.

Materials and Methods

Aurelia aurita and other forms

Literature-based comparisons were made using the European form, *Aurelia aurita*, and are denoted traditionally (*e.g.*, *Aurelia aurita*). The full breadth of literature used for comparison is too massive to list here, but can be found in the synonymies of Mayer (1910), Kramp (1961), and Russell (1970).

Literature-based comparisons were made with *A. flavidula* from the eastern United States, primarily following Agassiz (1862) and the references in the synonymy of Mayer (1910).

Literature-based comparisons were made to the boreal *A. limbata* using Brandt (1835, 1838), Vanhöffen (1906), Kishinouye (1910), Bigelow (1913, 1920), Uchida (1934), Bigelow (1938), Kramp (1942), Stiasny and van der Maaden (1943), Naumov (1961), Uchida and Nagao (1963), and Faulkner (1974).

Comparisons were made using live, captive medusae descended from a Japanese population (cultured at Cabrillo Marine Aquarium); although the phylogenetic relationship between the European and Japanese forms is still in question, they are structurally similar—that is, they both lack the enlarged manubrium characteristic of *A. labiata*.

Comparisons were also made on some live, wild medusae from Spinnaker Bay, Long Beach, California, which possessed the *A. aurita* body form, and on the descriptions of Greenberg *et al.* (1996) for the introduced San Francisco Bay form. Live representatives of Greenberg's population at Foster City could not be found. References made to forms that possess the *A. aurita* body type but are of uncertain taxonomic affiliation are denoted non-traditionally (*e.g.*, *Aurelia* "aurita" or *Aurelia cf. aurita*). This includes the captive Japanese form, as well as introduced forms.

Systematics of Aurelia labiata

Attempts were made to locate the holotype at the following institutions: The California Academy of Sciences (San Francisco) (CAS), Institut Royal des Sciences Naturelles de Belgique (Brussels), Museum für Naturkunde (Berlin), Muséum National D'Histoire Naturelle (Paris), Museum of Comparative Zoology (Harvard), Nationaal Natuurhistorisch Museum (Leiden), National Museum of Natural History (Washington), Natural History Museum (London), Zoological Institute (St. Petersburg), Zoological Museum (Copenhagen), and the Zoological Museum (Moscow University). All would have been reasonable depositories or recipients of a transfer of a holotype of a California species found by European explorers on a Russian expedition of that time. However, none had *A. labiata* type material nor knew where it might be kept; indeed, it appears doubtful that specimens were originally collected and deposited. Thus, my observations were made on animals from near the type locality and from many other regions along the Pacific Coast of North America.

A neotype was designated in order to stabilize the taxonomy of the species, and is deposited in the California Academy of Sciences in San Francisco. The original type locality could not be identified. Chamisso and Eysenhardt (1821) recorded the species from "New California," and a map in Schweizer (1973) indicates only somewhere near San Francisco Bay. However, specimens that I collected near San Francisco Bay were in poor shape, so the most intact representative specimen from the available material was selected from Monterey Bay (*ca.* 100 miles to the south). Morphological differences were not apparent between specimens from San Francisco and Monterey, excepting those attributable to collection.

I preferentially examined live medusae in the wild to avoid artifacts of captivity and preservation; however, cultured and captive medusae were observed supplementally.

In the wild, mature and immature medusae were collected from July 1995 to March 2000 by hand and by dip nets from nine locations in California (Coronado Island, San Diego; Newport Beach; Spinnaker Bay, Long Beach; Catalina Island; Marina del Rey; Santa Barbara; Monterey Bay; Sausalito, San Francisco Bay; Tomales Bay), and from Newport, Oregon; Poulsbo, Washington; Friday Harbor, San Juan Island, Washington; and Brentwood Bay, Saanich Inlet, British Columbia. Cultured and captive medusae were examined at the Birch Aquarium at Scripps, San Diego, California (San Diego *A. labiata*); Cabrillo Marine Aquarium, San Pedro, California (both Japanese *Aurelia* "aurita" and Long Beach *A. labiata*); Monterey Bay Aquarium, Monterey, California (Japanese *A. "aurita"* and Monterey *A. labiata*); Oregon Coast Aquarium, Newport, Oregon (Japanese *A. "aurita"* and Newport *A. labiata*); Point Defiance Zoo and Aquarium, Tacoma, Washington (*A. labiata* from Poulsbo, Washington); and the Seattle Aquarium, Seattle, Washington (*A. labiata* from Poulsbo, Washington). In addition to the above observations, characters were assessed as much as possible from a videotape taken in July 1996 of medusae from Prince William Sound, Alaska; from photographs of *A. labiata* from Steamer Bay, Alaska (Barr and Barr, 1983) and *A. limbata* from Amchitka Island, Alaska (Faulkner, 1974); and from preserved specimens from the Farallon Islands, California.

Measurements were taken on 7–20 live medusae from each of the following locations: Coronado Island, Newport Beach, Spinnaker Bay, Marina del Rey, Monterey Bay, Tomales Bay, Newport (OR), Poulsbo, and Brentwood Bay. Each medusa was individually dipped out of the water with a bucket and measured immediately with a vernier caliper or ruler to the nearest millimeter. Bell diameter (BD) was typically measured with the specimen lying flat on its ex-umbrellar surface. Manubrium length (ML) was usually measured with the animal in the water with the manubrium projecting upward, but captive medusae from Newport (OR) were measured with the manubrium hanging downward in the water. Since the manubrium is stiff and cartilaginous, its position did not appear to bias the measurements. To account for the difference in size at maturity of medusae from different populations, manubrium lengths were normalized as a percentage of bell diameter.

In addition to the measurements described above, about 200 medusae from each population were cursorily examined for the following characters, then released: manubrium shape, number of marginal scallops, oral arm length, number of radial canals emanating from each gastro-genital sinus, bell shape and color, and if female, the location and pattern of larval brood.

German papers were translated with Power Translator 6.02 for Windows (Globalink).

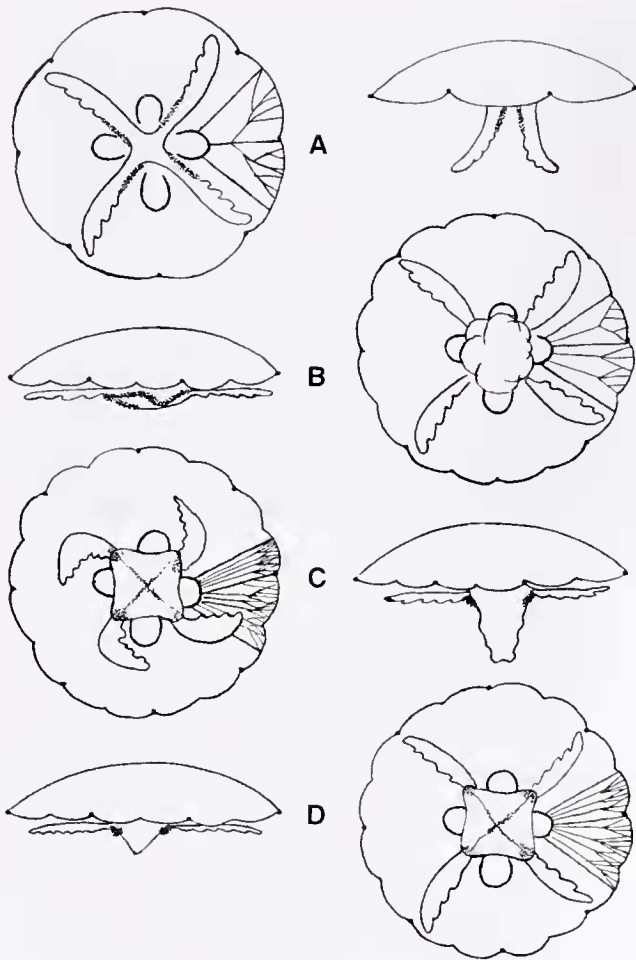


FIG. 3. Comparative diagram of three morphotypes of *Aurelia labiata* with *A. aurita*, subumbrellar and lateral views. (A) *Aurelia aurita*. (B) Southern morph, from Southern California Bight. (C) Central morph, from Santa Barbara, California, to Oregon. (D) Northern morph, from Puget Sound, Washington, to Alaska. In *A. aurita*, manubrium is inconspicuous, oral arms meet in the middle, the radial canals are few, and the margin has 8 scallops. In *A. labiata*, the manubrium protrudes below the bell margin, which has 16 scallops, there are many radial canals, and the oral arms do not meet. Darkened areas along oral arms (*A. aurita*) and manubrium (*A. labiata*) indicate position of larval brood.

Results

Comparison with European Aurelia aurita (Fig. 3)

Medusae from every population that I studied in the eastern North Pacific differed from published descriptions of the European *A. aurita* but closely matched the original description of *A. labiata*. Specifically, the *A. labiata* body form is characterized by an enlarged, fleshy manubrium; oral arms arising from the base of the manubrium; planulae brooding upon the manubrium; up to 15 radial canals arising from each gastro-genital sinus, and typically anastomosing in older individuals; and secondary scalloping of the bell margin between rhopalia (Fig. 3B-D). In contrast, the *A.*

aurita body type possesses no such enlarged manubrium structure; the oral arms meet in the middle of the animal; planulae are brooded upon the oral arms; typically only 3-5, sometimes 7, radial canals arise from each gastro-genital sinus; and secondary scalloping is rarely observed (Fig. 3A).

Comparison with western Atlantic Aurelia "flavidula"

The nominal species *Aurelia flavidula* is another taxonomic tangle that was somewhat resolved by Kramp (1942). Kramp concluded that the yellow Greenlandic form seen by Fabricius (1780) and named by Peron and Lesueur (1810) was identical to *A. limbata*, later named by Brandt (1835), and that calling the northern Atlantic American form *A. flavidula* was a mistake by Agassiz (1862). Agassiz had differentiated the western Atlantic *A. "flavidula"* from the European *A. aurita* on the former having a marginal network of anastomoses, the gonadal pouches closer together and occupying fully 1/3 of the bell diameter, and differences in the mouth fringes. Kramp further cautioned that using the name *A. flavidula* would be confusing, so he gave the common American Atlantic form the name *A. occidentalis*, distinguishing it from *A. aurita* on the heavier anastomosing of the radial canals; he later lumped it into *A. aurita* without comment (Kramp, 1961).

Proper phylogenetic placement of both the Greenlandic form and the common American Atlantic form must await a revision of the genus *Aurelia* based on live material. For the Greenlandic form, being yellow and having anastomosed canals seem insufficient for concluding conspecificity with the Alaskan *A. limbata*. Ideally, conspecificity should be based on numerous characters inherited by common descent, not by shared color. The importance of anastomosed canals is discussed below. The American Atlantic form, regardless of its identity, does not possess the enlarged manubrium and related characters of *A. labiata*; whether it is present along the Pacific coast of North America has not yet been determined.

Systematics of Aurelia labiata

The common moon jellyfish found in 17 populations from San Diego, California, to Prince William Sound, Alaska, is characterized by the body form described by Chamisso and Eysendardt (1821) for *A. labiata*. Many of the references to *Aurelia* of the eastern North Pacific do not contain illustrations or photographs; those that do are most often based on the European morphology. In at least one example, the same photograph is used in both West coast and East coast American field guides (Audubon Society, 1981). A large body of literature has thus been responsible for perpetuating the misidentification. The synonymy below contains only the references that have figures or descriptions positively referable to *A. labiata sensu* Chamisso and

Eysenhardt, 1821; thus, even references to *A. labiata* are not included below if they do not include the enlarged manubrium. The remainder of references to eastern North Pacific *Aurelia* are dealt with below in appropriate sections.

***Aurelia labiata* Chamisso and Eysenhardt, 1821
(Figs. 2; 3B-D)**

Aurelia labiata Chamisso and Eysenhardt, 1821: 358, pl. 28, fig. 1A, B.—Mayer, 1910: 622, 628, in part, eastern North Pacific records only.

Medusa labiata.—Eschscholtz, 1829: 64.

Aurelia labiata.—de Blainville, 1834: 294, pl. 42, figs. 1, 2 (Cham. & Eysen. illustrations).—Lesson, 1843: 377.—L. Agassiz, 1862: 160.—A. Agassiz, 1865: 43.—Haeckel, 1880: 557 (monograph).—Fewkes, 1889a: 593 (Point Conception, Monterey; manubrium).—Torrey, 1909: 11 (colf. by Cham. & Eysen.).—Barr and Barr, 1983: 80, text fig. 28 (Field Guide (= FG): AK).—Wrobel and Mills, 1998: 55 (FG: Pacific coast).—Gershwin, 1999: 993-1000, in part (symmetry variation).

Aurelia labiata non Linnaeus 1758.—Hauser and Evans, 1978: 21 text photo, 81 (commensal crab).—Snively, 1978: 152 text fig., pl. 77 (FG: BC, WA, OR).—Gotshall, 1994: 24, fig. 40 (FG).

Aurelia sp.—Campbell, 1992: 12, 13, Back cover (photographs).—Greenberg *et al.*, 1996: 401-409, in part, text fig 3, 4 (allozymes).

Moon jellyfish.—Malign, 1985: 40 (photograph).—Steffoff, 1997: 9 (photograph).

Holotype. Apparently not extant.

Neotype. CASIZ 111024, Monterey Bay, CA, coll. 19 April 1997 by D. Wrobel; gravid female, preserved 25-cm bell diameter (BD), 12-cm manubrium length (ML).

Additional preserved material. CAS 20, Farallon Islands, East Landing, coll. 14 Sep 1975 by D.R. Lindberg. CAS 95506, same data as CAS 20. CAS 95507, same data as CAS 20. CAS 81306, Monterey Bay, Pacific Grove, coll. 13 Nov 1990 by N. Greenberg, *ca.* 15-cm BD, manubr. 6.5 cm. CAS 81307, Monterey Bay, Pacific Grove, coll. 13 Nov 1990 by N. Greenberg, BD *ca.* 15 cm, ML *ca.* 6 cm. CAS 86767, 2 specimens, Vancouver Island, Sooke Basin, Roche Cove, coll. 11 Sep. 1990 by N. Greenberg, 14.5-cm BD, 6 cm ML. CAS 81304, Monterey Bay, Pacific Grove, coll. 13 Nov 1990 by N. Greenberg, *ca.* 13-cm BD, *ca.* 4-cm ML. CAS 81306, Monterey Bay, Pacific Grove, coll. 13 Nov 1990 by N. Greenberg. CAS 107800, 2 specimens, Monterey (CA), coll. 30 July 1966 by Rofen. CAS 111016 and 111020, Brentwood Bay, Saanich Inlet, coll. 24 June 1996 by LG. CAS 111017, Point Defiance, Puget Sound, coll. 5 April 1996 by LG. CAS 111021-111022, numerous specs, Santa Barbara, coll. 30 Nov 1996 by S. Anderson. CAS 111023, numerous specs, Marshall dock, Tomales Bay (CA), coll. 30 June 1996 by LG. CAS 111227, Spinnaker Bay, Long Beach (CA), coll. Sep 1995–Jan 1997 by L. Gershwin. In addition, preserved, unregistered specimens were examined from collections at Bodega Marine Laboratory, Cabrillo Marine Aquarium, Friday Harbor Laboratory, and Santa Barbara Museum of Natural History.

Diagnosis. *Aurelia* with manubrium elongated, wide, protruding below the bell margin when viewed laterally. Oral arms shorter than bell radius, attached to base of manu-

brium, extending outward to bell margin or bent at 90° angle typically counterclockwise. Bell margin 16-scalloped, with a primary indentation at each of 8 rhopalia and a secondary indentation midway between rhopalia. Older individuals typically with many radial canals arising from each gastro-genital sinus; in some, the outer branches are greatly anastomosed. Embryos and larvae brooded on the manubrium or on stiff, shelf-like manubrial extensions, rarely on the oral arms.

Redescription.

Medusa. (Based on mature tetramerous individuals.) Bell typically quite flat at rest, in some subhemispherical; older individuals may have raised hump over gonadal region. Diameter at maturity ranging from 100 mm to 450 mm, depending on population. Manubrium fleshy, rigid; rectangular, pyramidal, or rounded in side view; variably ruffled at 4 corners; width approximately 1/3 of bell diameter; with stiffened, whorled, perradial mesogleal extensions. Index of manubrium length to bell diameter varying geographically, longest in Oregon ($x = 37.2\% \pm 3.6\%$; $n = 10$, Newport), shortest in southern California ($x = 16.7\% \pm 2.6\%$; $n = 7$, Spinnaker Bay, Long Beach). Oral arms 4, perradial, straight or curved at 90° angles typically counterclockwise (but occasionally variable), arising from base of manubrium; length short, reaching approximately to bell margin (thus only $\pm 1/3$ bell diameter); extending laterally outward against subumbrellar surface of bell. In older cultured individuals, oral arms may hang downward. Size of subgenital ostia varying, encircled by raised mesoglea in some individuals. Interradial and adradial canals typically unbranched; perradial canals branched once, or in large individuals the gastro-genital sinus may overgrow the trifurcation causing the perradial canal to appear unbranched. Eradial canals branched, 4-12 arising from each gastro-genital sinus. Some large specimens have conspicuous anastomoses of canals on outer third of bell. Gastro-genital sinuses interradian, 4, but varying from 1 to 8 (perhaps more), in rounded to flattened horseshoe-shaped or heart-shaped rings, with adaxially-pointing free ends. Bell with 16 marginal scallops produced by 8 primary indentations at rhopalia located along the perradial and interradian axes, with secondary indentations between adjacent rhopalia. Bell transparent and colorless in juveniles and young adults, becoming milky white, or tinted pinkish, purple, peach, or bluish in older medusae. Color of gonad pale pinkish or brownish in mature females, dark purple in mature males, but often appearing white in males ready to spawn.

Planula. Elliptical to elongated; ciliated. Color most often white, but other colors found in certain populations: lavender (Monterey), peach (Saanich Inlet), or yellow-ochre (Spinnaker Bay). Planktonic or benthic locomotion by ciliary movement. Brooded on manubrium or its whorls.

Scyphistoma. Polyps 2-3 mm in height, with oral disk 1-2

mm diameter. Manubrium short, cruciform. Septal funnels conspicuous. Typically with 16 tentacles, alternating shorter and longer; number of tentacles highly varied, often corresponding to symmetry of parent medusae, parent polyp, or offspring ephyrae. At Friday Harbor, Washington, and Santa Cruz Island, California, scyphistomae typically with 20 tentacles. Color whitish to pale pinkish-orange. Habit benthic, usually hanging downwards from underside of docks, mussel shells, or rocks. Asexual proliferation by side budding, stolon budding, or podocyst formation. See Chia *et al.* (1984) for a histological study of the neuromuscular system.

Strobila. Ranging from monodisk to polydisk with more than 20 developing ephyrae. Color varying with locality: cinnamon in southern California, buff in Monterey. Polyp remaining flesh-colored or whitish. Strobilation time about 7 days; easily induced with periods of chilling.

Ephyra. Diameter 2-3 mm at release. With 8 marginal arms, each with a terminal rhopalium flanked by 2 lappets. Nematocysts scattered over the exumbrellar surface. Number of arms and rhopalia highly varied, not always in correspondence with each other or within a clone. Color same as the strobila: cinnamon or pale buff.

Type locality. Monterey Bay, California.

Distribution. I have collected *A. labiata* from Saanich Inlet, British Columbia, to San Diego, California. To the north, I was able to confirm its presence in Prince William Sound, Alaska, from a videotape; the species has also been photographed at Steamer Bay, in southeast Alaska (Barr and Barr, 1983). Its range may extend southward into the waters off Baja California, Mexico. The species generally occurs in bays and harbors where it is easily collected from jetties and boat slips, but medusae have been observed drifting in open waters off Santa Barbara, California (S. Anderson, Univ. California Santa Barbara, pers. comm., Nov. 1996), near Monterey Bay, California (D. Wrobel, Monterey Bay Aquarium, pers. comm., Oct. 1996; D. Powell, Monterey Bay Aquarium, pers. comm., May 1997), off Newport, Oregon (D. Compton, Oregon Coast Aquarium, pers. comm., June 1996), and in Puget Sound (LG, pers. obs., June 1996). The polyps generally strobilate in early spring, and the medusae quickly mature, spawn, and die by mid-summer or early fall. In some years and in some localities, the population of medusae is present throughout the year (Spinnaker Bay, LG, pers. obs.; Monterey, D. Wrobel, pers. comm.).

Biogeography

Observations of 17 populations from San Diego, California to Prince William Sound, Alaska have shown that the species can be reliably subdivided into three easily distin-

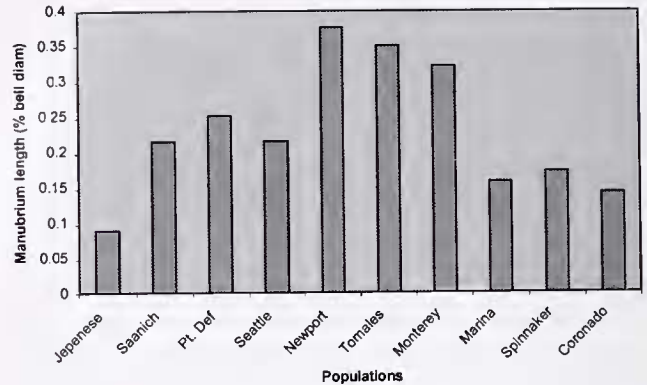


Figure 4. Average manubrium lengths of Japanese *Aurelia cf. aurita* and nine populations of *A. labiata*. Japanese = *Aurelia cf. aurita*, cultured at Cabrillo Marine Aquarium. Northern morph: Saanich = Saanich Inlet, British Columbia; Pt. Def. = Poulsbo, Washington (cultured at Pt. Defiance Aquarium); Seattle = Poulsbo, Washington (cultured at Seattle Aquarium). Central morph: Newport = Newport, Oregon (captive at Oregon Coast Aquarium); Tomales = Tomales Bay, California; Monterey = Monterey, California. Southern morph: Marina = Marina del Rey, California; Spinnaker = Spinnaker Bay, California; Coronado = Coronado Island, California. Between morphotype comparison, ANOVA; $F = 42.595$, $df = 3.5$, $P = 0.001$.

guishable geographical morphotypes. Though bell diameter is highly variable with environmental conditions, even among nearby populations (Lucas and Lawes, 1998), manubrium length, expressed as a percentage of bell diameter, differs significantly among the three forms (Fig. 4, ANOVA; $F = 42.595$, $df = 3.5$, $P = 0.001$). These three forms are easily distinguished as follows (summary in Table 1). Following the synopsis of each form is a list of literature that pertains to *Aurelia* from the region, but contains insufficient information for positive determination.

Southernmost form (Fig. 3B). Manubrium a wide, rounded frilly mound, not distinctly pyramidal. Radial canals few to many, possibly dependent on age; adradials particularly wide in San Diego medusae. Oral arms typically straight, not curved. Planulae ranging in color from white to ochre to bright orange, brooded in a reticulating pattern on frills of manubrium. Bell colorless to milky whitish; some individuals with dark purple tentacles. Male gonads dark purple, female gonads pale pink. Typical maximum size, 35 cm. Marina del Rey medusae with pronounced rhopalial hoods set up off the margin.

Known range. California, from San Diego to Marina del Rey, possibly extending north to Ventura and south into Baja California. Populations are apparently isolated and discontinuous; not observed at Oceanside, Dana Point, Los Angeles Harbor, or Malibu. Reported at Catalina Island. Local residents at Ventura Harbor and Channel Islands Harbor tell of seeing an occasional medusa or two; it is currently unclear if they are this form. Typically occurring until late spring, occasionally into autumn.

Table 1

Comparison of morphotype characters, *Aurelia labiata*

| Character | Northern morph | Central morph | Southern morph |
|---|------------------|------------------------|-------------------------|
| Manubrium length (\bar{x}) (as % bell diam) | 22.98% | 37.15% | 16.73% |
| SD | $\pm 0.04\%$ | $\pm 0.04\%$ | $\pm 0.03\%$ |
| <i>n</i> | 26 | 10 | 7 |
| site | Poulsbo/Saanich | Newport | Spinnaker Bay |
| Manubrium shape | pyramidal | long and tapered | rounded |
| Oral arm length | 1/3 bell diam | 1/3+ bell diam | 1/3 bell diam |
| Oral arm shape | \pm straight | counterclockwise | straight |
| # canals per sinus | 7-9 | 7-15 | 5-7 |
| Anastomosing | heavy | very heavy | moderate |
| Bell size | to 12 cm | to 45 cm | to 25 cm |
| Bell color | whitish or peach | purple, pink, or white | whitish |
| Planula color | white or peach | white or purple | white, ochre, or orange |

Literature.

Aurelia aurita.—MacGinitie and MacGinitie, 1949: 131, text fig. 32 (growth, strobilation, Newport Bay).—MacGinitie and MacGinitie, 1968: 131, text fig. 32 (growth, strobilation, Newport Bay).—Reish, 1972: 25, text fig. 26 (FG: Southern CA).—Allen, 1976: 22, 75 (FG: Southern CA).—Reish, 1995: 38, fig. 31 (FG: Southern CA).

Central form (Fig. 3C). Manubrium extremely elongated, rectangular and tapering. Canals numerous, typically heavily anastomosed in largest individuals. Oral arms straight or bent counterclockwise. Planulae distinctly lavender, brooded in teardrop-shaped clumps on the base of manubrium or on shelves. Scyphistomae pale buff colored. Medusae from Monterey, California tending to be distinctly purple; Santa Barbara, California, medusae often pale pink. Gonads dark purple in males, pale brown in females. Diameter of captive medusae from Newport, Oregon, recorded to 45 cm, with longest manubrium being 17 cm!

Known range. Santa Barbara (including Channel Islands), California to Newport, Oregon. Likely occurring, but unconfirmed, along the outer coast of southern Washington state. Abundant in late summer.

Literature.

Aurelia labiata.—Fewkes, 1889b: 122 (Santa Barbara Channel; pink).—Boyd, 1972 (fouling organism; Bodega Harbor, CA).—Pearcy, 1972: 354 (Oregon).—Hand, 1975: 95 (FG: Central CA).

Aurelia aurita.—?Galigher, 1925: 94 (scyphistomae; Monterey, CA).—Hamner and Jenssen, 1974: 833-848, text fig. 1 (growth and degrowth, Tomales Bay, CA).—Shenker, 1984: 619-630 (abundance; OR).—Abbott, 1987: 28 (morphology; Monterey).—Keen and Gong, 1989: 735-744 (scyphistoma clonal growth; Tomales Bay, CA).—Niesen, 1997: 43 (FG: Northern CA).—Rigsby, 1997: 207 (Monterey Bay).

Aurelia labiata.—Light *et al.*, 1954: 41 (FG: central CA).

Aurelia aurita.—Hedgpeth, 1962: 52, text fig. B (FG: Northern CA).

Aurelia sp.—Gottshall *et al.*, 1965: 149 (prey of blue rockfish; Bodega, Monterey, Morro Bay).—Pereyra and Alton, 1972: 448 (near Columbia River, OR).

Northernmost form (Fig. 3D). Manubrium low, pyramidal. Many parallel radial canals in mature individuals, giving a lacy appearance to the bell. Oral arms more or less straight, but may be variable in the same individual in

Departure Bay specimens (M. Arai, Pacific Biological Station, Nanaimo, BC, pers. comm. 2000). Planulae variably colored; brooded at the base of the manubrium and on manubrial shelves. Overall coloration peach or whitish, with gonads dark purple in males, pale brown in females. At Poulsbo, Washington, maximum diameter approximately 12 cm; brooded planulae white, appearing as a wash or haze rather than in discrete bundles. At Saanich Inlet, British Columbia, medusae larger, to approximately 15-cm diameter during my study, but reported to range from 14-29-cm (Hamner *et al.*, 1994); brooded planulae peach-colored.

Known range. Puget Sound, Washington, to Prince William Sound, Alaska; mainly occurring in late spring.

Literature.

Aurelia labiata.—Carl, 1963: 101 (FG: BC).—Kozloff, 1974: 22, in part (FG: WA).

Aurelia limbata.—?Stiasny, 1922: 522 (Vancouver).—?van der Maaden, 1939: 33 (rhopalial folds; Vancouver).

Aurelia aurita.—Bigelow, 1913: 98 (marginal scallops; Puget Sound).—Clemens, 1933: 16 (Canada).—Kozloff, 1973: 62, text photo 10 (FG: WA).—Arai and Jacobs, 1980: 120 (medusivory; BC).—Mills, 1981: 22 (seasonality; Puget Sound).—Kozloff, 1983: 56, text photo 13 (FG: WA).—Chia *et al.*, 1984: 69-79 (scyphistoma structure; Puget Sound).—Larson, 1986: 107-120 (chemical composition; Saanich Inlet).—Kozloff, 1987: 65 (FG: Pacific Northwest).—Larson, 1987: 93-100 (carbon cycling; Saanich Inlet).—Strathmann, 1987: 76 (development; Puget Sound).—Strand and Hamner, 1988: 409-414 (prey of *Phacellophora*, Saanich Inlet).—Norris, 1989: 381-393 (fossilization).—Arai, 1991: 363 (chemical predation cues; BC).—Keen, 1991: 1-176 (scyphistoma biology; Tomales Bay).—Fautin and Lowenstein, 1992: 13 (polyp and medusa proteins).—Hamner *et al.*, 1994: 347-356 (sun migration; Saanich Inlet).

Aurelia sp.—MacGinitie, 1955: 120 (color range; Pt. Barrow, AK).—Zubkoff and Lin, 1975: 915 (isozymes).

In addition to the literature apparently attributable to each form above, a large body of literature exists which pertains to *Aurelia* of the eastern North Pacific but cannot be attributed to a single region as described above. Many of these references do not illustrate the species, or in some cases, use general drawings or photographs from other locations.

Aurelia aurita.—Johnson and Snook, 1927: 82, text fig 62 (FG).—Guberlet, 1936: 45, text photo (FG; Northwest).—Guberlet, 1949: 45, text photo (FG; Northwest).—Hartman and Emery, 1956: 307 (CA).—Guberlet, 1962: 45, text photo (FG; Northwest).—Flora and Fairbanks, 1966: 50, Fig. 42: (FG: BC, WA, OR).—Johnson and Snook, 1967: 82, text fig 62 (FG).—Brusca and Brusca, 1978: 52, text fig. 22 (FG: CA).—McLachlan and Ayres, 1979: 47, text photo (FG: Pacific Northwest).—Gotshall and Laurent, 1980: 40, text photo 40 (FG, Pac. coast).—Haderlie *et al.*, 1980: 52, pl. 3.22 (FG: CA).—Audubon Society, 1981: 363, in part, pl. 502 (photo is of *A. aurita*, possibly outside NE Pacific).—Austin, 1985: 71 (Alaska to southern California).—McConnaughey and McConnaughey, 1985: 466, pl. 384 (photo is of *A. aurita*, but may have been taken elsewhere).—Ricketts *et al.*, 1985: 303, text fig. 316 (FG).—Farmer, 1986: 111 (FG; AK to so. CA).—Parsons, 1986: 18 (sting treatment).—Connor and Baxter, 1989: 53 (in kelp forest).—Amos, 1990: 36, in part, Alaska to southern California (photo is of *Aequorea* sp. (Cnidaria: Hydrozoa) but attributed to *A. aurita*).—Larson, 1990: 546-556 (distribution).—Larson and Arneson, 1990: 130-136 (California).—Niesen, 1994: 48, text fig. 4-33 (FG: CA).—Thuesen and Childress, 1994: 84-96 (enzyme activity; southern and central CA).

Aurelia (and *Aurelia* sp.).—Ricketts and Calvin, 1939: 244, text fig. 109 (FG).—Wells, 1942: 146, text fig. (FG).—Ricketts and Calvin, 1948: 144, 244, text fig. 109 (FG).—Ricketts and Calvin, 1952: 328, text fig. 109 (FG).—Smith, 1962: 13, text fig. 10 (FG: Pac. Northwest).

Aurelia aurita.—Light, 1941: 19 (invert. manual).—Ricketts and Calvin, 1968: 264, text fig. 266 (FG).

Aurelia (and *Aurelia* sp.).—Tierney *et al.*, 1967: 26, text fig. (FG).

Jellyfish.—Ulmer, 1968 (children's book).

Aurelia labiata.—North, 1976: 153 (FG: CA).—Austin, 1985: 71 (Alaska to central CA).

A second *Aurelia aurita* introduction

A second population of *Aurelia aurita*, apparently introduced, has recently been found at Spinnaker Bay, Long Beach, California (the first was found at South San Francisco Bay, California, by Greenberg *et al.*, 1996). It is impossible to know exactly when it first appeared; however, I have been working closely with the Spinnaker Bay population since 1995, and have only observed this other form since 1997. Morphologically, it is allied to the European and Japanese forms. However, preliminary 18S rDNA partial sequence analyses indicate that it is similar to a population from Fort Lauderdale, Florida (J. Lowrie, Cnidarian Research Institute, pers. comm., June 2000). Lowrie has further found that the Spinnaker Bay population clusters into at least four genetic subpopulations, one closely related to island populations, one as described above, and two apparent hybrid forms. This pattern is evident in the morphology as well. Since 1997, both *A. labiata* and *A. aurita* medusae have been observed side by side, as well as some that possess characters of both.

Comparison with Japanese *Aurelia aurita*

The Japanese form of *A. aurita* closely matches the descriptions of the European form (*e.g.*, Russell, 1970), and thus differs morphologically from *A. labiata* in a similar manner. Kishinouye (1891) described a form from Tokyo Bay, Japan, named *Aurelia japonica*; it was said to differ

from *A. aurita* in having prominent subgenital cavities and in having broad and folded lobes on the proximal halves of the oral arms (Kirkpatrick, 1903). Whether this form is identical to the European form or to *A. flavidula*, or to the Japanese material presently raised in American public aquariums, has not yet been determined and is beyond the scope of this paper.

Notes on *Aurelia limbata*

Upon casual inspection, *A. limbata* appears to be unmistakable because of its chocolate-brown marginal pigment band (see Audubon Magazine, Jan. 1974 cover, for an excellent photograph). It also appears to be distinctive in having relatively few tentacles and in the extreme anastomosing of the radial canals in all growth stages. However, closer examination may show *A. limbata* of the Arctic to be a fourth morph of *A. labiata*, or possibly even a color variant of the northern form. Mayer (1910) regarded *A. limbata* as a variety of *A. labiata*, apparently based on its having 16 marginal scallops. I have not had the opportunity to examine specimens of *A. limbata*, but written descriptions, drawings, and photographs reveal additional similarities. Like the northern form of *A. labiata*, *A. limbata* has a triangular protruding manubrium and many radial canals emanating from each gastro-genital sinus (Kishinouye, 1910; Faulkner, 1974; but the former character is not apparent in Mertens's illustrations published by Brandt in 1838). In addition, *A. limbata* shares with the Marina del Rey, California, population of *A. labiata* the peculiar character of large and conspicuous rhopalial hoods that are well above the bell margin. There has been some debate about the phylogenetic meaning of wrinkles in the rhopalial pits (see Uchida, 1934; van der Maaden, 1939); this character has not been checked in *A. labiata*. Furthermore, the anastomosing of the radial canals is far more developed in *A. limbata*. If the two nominal species are eventually regarded as conspecific, the name *A. labiata* would have chronological priority. More logically, *A. limbata* may be a separate species in an undefined species complex currently known as *A. labiata*.

Discussion

Biogeographical and systematic implications

Most twentieth century authors regard *Aurelia aurita* as cosmopolitan, occurring abundantly the world over, and some recognize *Aurelia limbata* of the Arctic Ocean as the only other species in the genus. These notions are dispelled by the present results. Not only is *A. aurita* replaced along the American Pacific coastline by *A. labiata*, but the latter is also divided into three morphologically distinctive forms coincident with established bioprovinces. Furthermore, there is some evidence that *A. limbata* may be a color morph

or possibly even a separate species within the clade currently known as *A. labiata*. Thus, the *Aurelia* group may actually consist of numerous local species, as was indicated by Lambert (1935), Hummelinck (1968), Hamner and Hauri (1981), and Brewer (1991) for other taxa, or possibly even more than one genus. Future molecular analysis of the morphotypes may elucidate the degree of differentiation.

One of the predictions of this hypothesis is that additional populations of *Aurelia* found along the Pacific coast of North America may be assignable among the three morphotypes, according to morphology and latitude. The eastern North Pacific flow patterns are consistent with the morphological differences of the jellyfishes, with both currents and morphologies diverging in the vicinity of Point Conception, California, and Puget Sound, Washington. The three regions corresponding to the morphotype ranges are coincident with the Californian, Oregonian, and Aleutian bioprovinces of molluscs (Hall, 1964: fig. 5; see also Valentine, 1966: fig. 1). Although molluscan provinces appear to be determined by sustained reproductive water temperatures (Hall, 1964), the cause of similar distribution in *Aurelia* is currently without explanation. Logically, temperature could play a role, but *Aurelia* is able to grow and reproduce continually in the laboratory in a wide range of temperatures, both cooler and warmer than the ambient ocean temperature (unpubl. notes). It is well documented that the distributions of benthic groups such as molluscs (Campbell and Valentine, 1977; Roy *et al.*, 1998) and algae (Abbot and Hollenberg, 1976) conform to biogeographical provinces. In contrast, the ranges of pelagic taxa are typically thought to be ill-defined at the fine scale, being confined primarily by the great gyres, if not cosmopolitan (Lalli and Parsons, 1993; Nybakken, 1993). For a nearshore pelagic invertebrate such as *A. labiata*, this generalization does not hold true. Further studies should examine *Aurelia* and other widespread coastal medusae in regions with similar latitudinal gradients, that is, eastern and western continental shores in both hemispheres.

Several recent studies may become important in our understanding of nearshore medusa distribution. First, Hellberg (1996) examined differential gene flow between one coral species that brooded its larvae and another with pelagic, feeding larvae; he found greater genetic subdivision in the brooding species. Likewise, *Aurelia* spp. and *Cyanea* spp. are planula brooders, and thus may have less gene flow among populations than previously assumed. Second, Cowen *et al.* (2000) found that simulated larvae do not disperse as readily as generally thought. Indeed, it appears that dispersal in some cases may be overestimated by nine orders of magnitude. Medusae, like larvae, are not passive particles. Rather, their dispersal ability is subject to their own behaviors as well as to diffusion and mortality. Many medusae swim actively against a gentle current, or drop lower in the water column to avoid currents (pers. obs.);

these behaviors may serve as anti-dispersal mechanisms. Finally, Barber *et al.* (2000) found a sharp genetic break in nearby populations of the mantis shrimp *Haptosquilla pulchella* in Indonesia, and suggested the presence of a sort of "marine Wallace's line." Even though the stomatopod larvae are planktonic, and thus have the means to disperse over great distances, it appears that they do not. Whether the same explanation can be applied to *Aurelia* remains to be shown.

Because so much of the coastline is hospitable to *A. labiata*, it is helpful to ask whether other similar species may be present as well. Currently there is no evidence of endemic species other than *A. labiata*, excepting the unresolved nomenclatural questions relating to *A. limbata*. However, it is easy to imagine that other forms may have been overlooked in a similar way as *A. labiata*, or that within the species I herein recognize as *A. labiata*, numerous cryptic species exist. The recent scientific literature abounds with discoveries of cryptic species, such as one recent startling example, wherein the fungal *Gibberella fujikuroi* species complex was found to comprise 45 phylogenetic species (O'Donnell *et al.*, 1998)! Given that many of the populations of *A. labiata* along the eastern North Pacific coast are uniquely diagnosable, and that these diagnosable forms partition into the three latitudinal morphotypes, the possibility of cryptic species seems high. Indeed, Greenberg *et al.* (1996) hypothesized restricted gene flow between eastern Pacific populations, based on significant allele frequency differences. Thus, the biogeographic pattern in *A. labiata* may represent cladogenesis in action, or possibly even a splitting event of the recent past. I hesitate at this time to recognize the three forms as distinct species, or for that matter to assign the eastern North Pacific forms to a new genus, although it is clear that the three forms are quite different from one another and from *A. aurita*. Although scyphozoan population genetics have not yet been studied in depth, some cnidarians have surprisingly low rates of genetic divergence (see Knowlton, 2000), so species conclusions should be made cautiously. Thus, until the clade currently known as *A. aurita* is resolved, it is difficult to comment with confidence on the internal and external relationships of the morphotypes of *A. labiata*. However, this does beg the questions of species concept and species recognition criteria.

Taxonomic characters

Throughout most of the twentieth century, it was customary to recognize medusan taxa based on certain key characters, regardless of distribution and discrete forms of variation; that is, all populations possessing a small number of given characters were thought to be one species. For example, in the Pelagiidae, the character of tentacle number has been so highly regarded that a large and conspicuous spe-

cies was incorrectly classified, favoring a tentacle number over all other characters combined (Gershwin and Collins, 2001). The same reasoning seems to have applied to *Aurelia*, favoring the "essence" of *A. aurita* over all other characters. This appears to have resulted in excessive lumping for many taxa. In contrast, I have employed a phylogenetic perspective, bringing together data from morphology, geography, and genetics to evaluate a lineage's history. However, some characters are still worthy of further comment, as they have led to confusion in the past.

Perhaps the most ignored character is the best key in separating *A. labiata* from *A. aurita*. Greenberg *et al.* (1996) used manubrium length in distinguishing the American form from the Japanese form, but failed to notice the associated changes in the relationship of the oral arms to each other and the altered brooding habits (Figs. 1, 2, 3B-D). To summarize, in *A. labiata* the oral arms are relatively short, about one-third the bell diameter, and project outward from the base of the fleshy manubrium. In addition, the larvae are brooded on the manubrium or on the rigid manubrial shelves. In contrast, *A. aurita* lacks the fleshy manubrium; consequently, the oral arms meet at the mouth and are about one-half the bell diameter. Furthermore, the brood pouches for the larvae line the upper portions of the oral arms. Thus, the large manubrium of *A. labiata* relates to a suite of morphological and functional differences from *A. aurita*.

Kramp (1913) considered the anastomosed canals to be a distinctive character in separating the Greenlandic form of *A. aurita* (as *A. flavidula*) from the typical form, and most descriptions of *A. limbata* include this character. However, the canals of some captive medusae of both *A. labiata* and *A. "aurita"* eventually become heavily anastomosed (F. Sommer, Monterey Bay Aquarium, pers. comm., and my own unpublished observations), possibly attributable to the phenomenon of growth and degrowth (Hamner and Jenssen, 1974). This was not taken into consideration by Greenberg *et al.* (1996), in claiming that the anastomoses could be used as a reliable character for distinguishing eastern Pacific *Aurelia* from western Pacific *Aurelia*. Indeed, their North American medusae were held captive nearly a year, whereas their Asian medusae were held only for 2 months. Although this character does seem more conspicuous in large specimens of *A. labiata* than in *A. "aurita"*, this may be due to the increased number of canals in *A. labiata*; that is, many canals anastomosing may give the appearance of a finer mesh than one would expect in an individual with fewer canals. This too (extra canals) was not taken into account by Greenberg *et al.* (1996). A closer study of anastomosis of canals might be helpful in future taxonomic studies.

Some authors have reported that the number of canals arising from the gastro-gonadal sinuses is taxonomically unreliable because it is associated with size and rate of growth (Stiasny, 1922; Bigelow, 1938; Kramp, 1942, 1965; Russell, 1970). Indeed, I have observed that older, larger

individuals do tend to have more canals than smaller, younger individuals. However, old, large *A. aurita* typically have 1 or 2 radial canals arising in each space between interradial and adradial canals (for a total of 5-7 canals arising from each gonad), whereas old, large *A. labiata* typically have 3-6 radials per side (for a total of 9-15 total per gonad). However, in the closely related *A. limbata*, Stiasny (1922) and Bigelow (1938) argued that the number of radial canals and the degree of branching are both useful characters. Curiously, medusae of the northern and central forms tend to possess greater numbers of radial canals than do medusae of the southern form.

The taxonomic significance of the 16-scalloped bell margin is currently unclear. Medusae from all endemic eastern North Pacific populations that I have observed possess this scalloping, in some cases quite conspicuously so. However, use of this character to distinguish species has been criticized by Kramp (1965), citing that in *A. limbata* the secondary scalloping is lost in preservation, and agreeing with Bigelow (1913) that the degree of scalloping is merely due to contraction of the bell. Because of its occasional occurrence in *A. aurita*, the secondary scalloping should not be used as the distinguishing taxonomic character of *A. labiata* as has been done in the past. However, it remains one of several useful field characters for *A. labiata* and may prove useful in similarly distinguishing other species worldwide.

Confusion has arisen regarding certain specimens from Nanaimo, British Columbia. Stiasny (1922) and van der Maaden (1939) assigned them to *A. limbata*; whereas Kramp (1942) identified them as a variety of *A. aurita* based on the width of their radial canals. I have not yet examined these specimens. However, Stiasny's (1922) description is consistent with *A. labiata*, namely, the 16-scalloped margin and the 5-9 radial canals issuing from each gastrovascular sinus.

At present, *A. labiata* appears to be a temperate endemic restricted to the eastern North Pacific. However, this leaves a series of references to medusae with 16 marginal scallops as *A. labiata*, although their morphological characteristics and geographic locations suggest that they are not. Available drawings and a photograph all clearly show 16 scallops of the margin, but do not show a protruding manubrium or numerous radial canals (Mayer, 1910, 1917; Uchida, 1928). Since the illustrations of Chamisso and Eysenhardt (1821) indicate a large manubrium, I exclude medusae that lack this character from this classification. However, I have not examined specimens from the following sources for complete diagnostic characteristics.

Aurelia labiata.—Mayer 1910: 628, fig. 398 (*A. limbata* as var. of *A. labiata*; Philippines).—Light, 1914a: 294 (harmless); Philippines).—Lie, 1914b: 200 (Philippines).—Mayer, 1915: 160, 182 (*A. labiata* derived from *A. aurita*).—Mayer, 1917: 205, text fig. 11 (Philippines and Tortugas, Florida).—Light, 1921: 31 (Philippines).—Bigelow, 1938: 167 (synonymous with *A. aurita*).

Aurelia labiata.—Stiasny, 1919: 93 (Malay Archipelago).—Stiasny,

1926: 244 (Philippines; *A. labiata* is a variety of *A. aurita*).—Uchida 1928: 373-376 (pentamerous, Palau).—Stiasny, 1931: 140 (specimen at British Museum).—Stiasny, 1935: 34 (Aroe Islands).—Stiasny, 1937: 207 (East Indies).—Ranson, 1945: 60, 61 (review of genus).—Kramp 1961: 340 (taxonomy).—Kramp, 1965: 262-263, plate 1 fig. 1 (*A. labiata* same as *A. aurita*).—Kramp 1968: 68 (discusses *A. labiata*).—Russell 1970: 140 (discussion of synonymy). Powell, 1975: 6 (New Zealand).

Two reports of *A. labiata* in Hawaii (Chu and Cutress, 1954: 9; Devaney and Eldredge, 1977: 111) are worthy of attention. Drawings I made in 1993 from live animals in the Waikiki Aquarium appear to be of *A. labiata*. However, preserved specimens from the same location examined in 1997 lacked the enlarged manubrium. At this time, I provisionally include Hawaiian *Aurelia* with *A. labiata*, but firm determination must wait until additional live and preserved material can be examined. The Oahuan form appears to be introduced, as it was not reported until 1954, but the origin of the introduction is not yet known (J. T. Carlton, Mystic Seaport, Mystic, CT, and L. G. Eldredge, B. P. Bishop Museum, Honolulu, HI, pers. comm.).

Thus far, little consensus exists over what characters are taxonomically reliable for jellyfishes over a wide range of populations. To further confound the problem, immature specimens of closely related species often bear a striking resemblance. However, recent rearing of Japanese *Aurelia* "*aurita*" and Monterey *A. labiata* in the same aquarium yielded distinctive morphs consistent with the two species (M. Schaadt, Cabrillo Marine Aquarium, San Pedro, CA, pers. comm., Oct. 1999). Although I have herein distinguished only the northern, central, and southern morphs, medusae from each of the 11 locations were easily identifiable. The ability to distinguish morphological characteristics associated with particular populations of *Aurelia* spp. will not only help to resolve the phylogeny of the group, but may also help in identifying the origins of introductions such as those in Spinnaker Bay, California; San Francisco Bay, California (Greenberg *et al.*, 1996); and Oahu, Hawaii (J.T. Carlton and L.G. Eldredge, pers. comm., 1998).

Field key to the eastern North Pacific forms of *Aurelia*

1. Bell lacking secondary notches between adjacent rhopalia, margin 8-scalloped. Lacking broad and/or elongated manubrium. Currently known only from South San Francisco Bay and Spinnaker Bay *cf. A. aurita*
 - 1'. Bell with secondary notches between adjacent rhopalia, appearing 16-scalloped. Possessing conspicuously broad and/or elongated manubrium 2
 2. Bell with conspicuous chocolate-brown margin. Primarily Arctic *A. limbata*
 - 2'. Bell lacking brown margin 3
 3. Manubrium greatly elongated, tapering rectangular in shape. Generally found Pt. Conception, CA, to northern Oregon. Color variable from white to purple to pink. Often very large, to 45 -cm or more . . . *A. labiata*, central morph

3'. With manubrium protruding in lateral view, but much less than one-third bell diameter 4

4. Manubrium pyramidal. Generally found in and north of Puget Sound. Color variable from white to peach. Typically small, 12-15 cm *A. labiata*, northern morph

4'. Manubrium rounded. Generally found south of Pt. Conception. Color typically milky white, occasionally with dark tentacles *A. labiata*, southern morph

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